

Long-Term Changes in Willow Distribution on the Winter Range of Rocky Mountain National Park

By

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Abstract. We determined the extent and spatial pattern of changes in willow (*Salix* spp.) cover in the riparian areas of the eastern slope of Rocky Mountain National Park (RMNP), Colorado, between 1937 or 1946 and 1996, and related these changes to suspected causative factors. The study was conducted in two watersheds of the north-eastern side of RMNP, which includes the Moraine Park area of the Big Thompson River watershed (2,481 m), and the Horseshoe Park area of the Fall River watershed (2,598 m). Changes in vegetation were inferred from digital maps generated from aerial photointerpretation and field surveys. Low-resolution digital maps were created based on old (1937 or 1946) and new (1996) aerial photos to determine the extent of willow decline. High-resolution digital maps of vegetation cover were created from a field survey conducted in the summer of 1998. In these maps, willow cover was described in terms of morphotypes (sapling, young short, old short, intermediate, and tall), density, and percentage of dead plants. Digital and attribute information were combined to produce maps.

The decrease in riparian shrub cover in Moraine Park was 21 ha (21%) and 17 ha (19%) in Horseshoe Park over the 50- or 59-year period. Reductions in the total length and surface water of the main river were 56% and 69% in Moraine Park and 44% and 47% in Horseshoe Park, respectively. Tall willow cover was found mainly in the upper areas of both valleys. Short old willow morphotypes were spatially distributed preferentially in areas affected by flooding in Horseshoe Park, and in areas where major river reductions were observed in Moraine Park. Both valleys had sites that were being colonized by willows, in wet meadows, and in the case of Horseshoe Park, open areas created by flood disturbance. The decline in tall willow cover corresponded to 54% and 65% in Moraine Park and Horseshoe Park, respectively, over 50–59 years.

Willow decline in Moraine Park was apparently the result of a reduction in water availability for growth. Over the last 50 years there has been a trend toward simplification of river spatial pattern, i.e., less complex branching and channelization, and a decrease in total water surface area in Moraine Park. The same trend in river morphology was documented in Horseshoe Park, but in that drainage, willow decline occurred mainly because of a large flood disturbance in 1982. In both valleys, surveys indicated a decline in beaver in excess of 90% since 1940. This has generated unfavorable conditions for willow growth. The causes of these fluvial changes were not determined, but were likely related to a decline in beaver populations and an increase in elk population (from approximately 700 to about 3,000 total elk, and from 500 to 1,000 elk within the park, during the study period). The elk increase has also placed increased browsing pressure on willow, which has led to a reduction in plant heights. Persistence of these riparian willow communities in their former abundance and extent may depend on the reestablishment of beaver.

Keywords: Beaver impoundments, elk browsing, hydrology, riparian areas, vegetation transitions, willow.

Introduction

Riparian vegetation comprises a small area of the landscape along river courses, in which the river has a major control on physical conditions (Tabacchi et al. 1990; Gregory et al. 1991). These areas are subject to periodic fluvial disturbances occurring because of flooding and/or migration of the active channel and meanders of the river (Bradley and Smith 1986; Gregory et al. 1991; Miller et al. 1995). Disturbance produces irregular patches of riparian vegetation types, arranged in a mosaic along the area of river influence (Miller et al. 1995). Non-fluvial disturbances are also common. These include fire, wind, plant disease, insect outbreaks (Gregory et al. 1991), herbivory by large mammals (Naiman 1988; Johnston and Naiman 1990a; Collins and Helm 1997), and beaver dams (Johnston and Naiman 1990b). Riparian areas have been extensively modified by human activities resulting in habitat degradation, which has affected both terrestrial and aquatic species composition (Décampus et al. 1988; Roth et al. 1996). Trends in cover and characteristics of riparian vegetation are often difficult to distinguish from the normal recurrent disturbance effects, so long-term analyses are required (Johnston and Naiman 1990c; Miller et al. 1995).

Documentation of temporal and spatial dynamics of landscape pattern has been greatly stimulated by the availability of new technological tools, in particular geographic information system (GIS) and remote sensing technology (Ustin et al. 1993; Johnson and Gage 1997). The comparison of historic and recent aerial photos at a medium level of resolution is a reliable, quantitative method for evaluating long-term vegetation changes, particularly when combined with GIS (Johnston and Naiman 1990c; Clemmer 1994). This approach was used here to analyze the temporal change of riparian shrub cover in two watersheds in Rocky Mountain National Park (RMNP), Colorado, and to make inferences about the factors that could drive vegetation change.

Willow (*Salix* spp.) dominates the riparian landscapes of the eastern slope of RMNP, forming a complex mosaic of patches of willow plants of different heights. A decline in willow abundance, distribution, and stature has apparently occurred on these areas. Three main hypotheses have been proposed for willow declines (Singer et al. 1998a): (1) higher grazing pressures on willow, caused by increases in the elk (*Cervus elaphus*) population; (2) warmer and drier climatic trends occurring during this last century; and (3) decline in beaver (*Castor canadensis*) population. Since humans

extensively used this study area and drained some areas in the park, human impact should also be considered among the probable causative factors.

In this report, GIS maps of riparian vegetation and hydrology of two closed watersheds of RMNP were generated at two scales of resolution (high and low-resolution digital maps). The analysis procedure was designed to answer the following set of questions: Has the spatial distribution of willow vegetation been reduced at the landscape scale? If so, what is the spatial pattern of willow decline, and what factors could be associated with this pattern? Since vegetation changes are normally controlled by a complex interaction of factors, we hypothesized that multiple causative factors might explain the overall changes in vegetation cover. However, factors could be hierarchical, with some of them primary and others secondary. Primary factors might override the effects of secondary factors. Some of the proposed factors that could produce changes in willow cover, for example, drier climatic trend, elk population increase, and beaver decrease, were similar in both study watersheds. Consequently, these primary factors would produce similar changes in the patterns of willow cover in both watersheds. However, any differences between watersheds would indicate that more localized primary factors are driving these changes.

Methods

Study Sites

The study was conducted in two watersheds of the northeastern side of RMNP which includes the Moraine Park area of the Big Thompson River watershed (2,481 m), and the Horseshoe Park area of the Fall River watershed (2,598 m). Vegetation in these valleys is composed of communities of riparian shrubs dominated by willow (*Salix monticola*, *S. geyeriana*, and *S. planifolia*), and in some areas by birch (*Betula* spp.). Meadows occur in several parts of the valley farther from the river course. Wet meadows are dominated by *Poa* spp., and dry meadows by *Carex* spp. and *Artemisia* spp. Vegetation communities dominated by trees represent a minor proportion of the total cover, and include conifers (*Pinus contorta* and *Pinus ponderosa*) and aspen (*Populus tremuloides*) communities. The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Mean annual precipitation for the sites is 41 cm (Singer et al. 1998a) and peak stream flow usually occurs in early to mid-June.

Historical Changes in Land Use, Elk, and Beaver

Native people camped and hunted in the valleys, mountains, and tundra of what is now known as RMNP since 3850 B.C. (Hess 1993). Trappers and explorers occasionally visited this area but it was not until 1859 that permanent settlement began (Hess 1993). The first record of settlers within current park boundaries was in 1875, when Abner Sprague built a cabin and grazed 200 cattle in Moraine Park, but in the 1880s and 1890s the Sprague Ranch expanded to 1,000 acres and shifted in focus from cattle to tourism (Buchholtz 1983). Moraine and Horseshoe Parks were not within the national park boundary when it was created in 1915. From the 1870s until the 1930s, ranches and resorts occupied much of Horseshoe and Moraine Parks (Buchholtz 1983). Horseshoe Park was incorporated into the national park boundaries in 1932. Stead's Ranch, the Moraine Park remnant of Abner Sprague's 1875 homestead, was purchased in 1962 by the National Park Service and returned to a natural meadow. This ranch at one time consisted of a 600-acre ranch, a lodge, barns, cabins, and a golf course (Buchholtz 1983).

Human activities have brought about important changes in the composition and characteristics of the vegetation. It is clear that drainage and irrigation ditches were built on Moraine Park, and remnants are still evident today. Ditches could have been used to drain overly wet areas and to irrigate hay fields and the golf course. The golf course was irrigated through at least 1961. An official Park Service report [1930] described conditions on the various ranges. In Moraine Park... "the whole area is grazed by domestic stock throughout the year and is badly overgrazed". This included the grassland areas. The meadow areas were again cut for hay and later used as pasture. "A heavy growth of willow" existed along the streams... Horseshoe Park was badly overgrazed [by livestock]. These comments indicate that grasses were being heavily used by livestock, but shrubs and trees were less affected" (D. Stevens, 1980, National Park Service, unpublished report). In Horseshoe Park, one of the main disturbances on riparian vegetation was the flood produced by the failure of the Lawn Lake Dam in 1982. Lawn Lake is located at treeline (3,350 m above sea level); downstream from Lawn Lake the Roaring River descends to join the Fall River in Horseshoe Park at an elevation of 2,605 m (Jarret and Costa 1993). Sediment from the Lawn Lake flood covered a willow carr community in Horseshoe Park, and in this area,

some of the material transported by the flood was deposited as an alluvial fan (Keigley 1993).

Wildlife has been extensively hunted since the arrival of the first European settlers. The winter range for elk in RMNP encompasses about 10,000 ha. This includes the two study valleys, as well as other valleys and private and national forest lands outside the park in the town of Estes Park and the Estes Valley, Colorado (Singer et al. 1998a). The elk had been hunted to extinction by 1900, but in 1913 and 1914, 49 elk from Yellowstone were transplanted to the park (Hess 1993). By 1942, elk had increased to approximately 1,500 individuals. A program of elk control by shooting animals, begun in 1944, reduced the population to around 400 individuals (Hess 1993). Since 1968, under the natural regulation policy, the elk population has increased to 3,000 individuals (Singer et al. 1998b), 1,000 of which winter in RMNP (Lubow et al., this volume).

Beaver were abundant in the areas of RMNP prior to European settlement, but they started to be intensively trapped in the mid-1800s (Hess 1993). "Exactly how many beaver pelts may have been extracted from the streams of RMNP during the fur trade era is unknown signs of the lucrative trade dotted the nearby region, allowing us to assume that trappers worked every likely drainage. By 1830 small trading posts began to appear... But just as these posts were built, men's fashion in hats changed... demand for beaver pelts declined, and within a decade [the]... forts were deserted" (Buchholtz 1983). Pressure on beaver did not seem to decline, however, and "in 1890 beaver was virtually eliminated from the adjacent valley of Estes Park" (Hess 1993). However, beaver were abundant in the national park when it was established in 1915 (Hess 1993). The first detailed surveys of beaver on the major drainages of the park, including the study area, were done in 1939 and 1940 (Packard 1947). Other surveys were done in 1964 (Hickman 1964), 1980 (Stevens and Christianson 1980), and 1994 to 1998 (Zeigenfuss et al., this volume). In all surveys, beaver populations were estimated indirectly from signs of beaver activities that were registered by walking on the stream bank. Surveys are problematic to compare; however, the estimates clearly indicate a declining trend over time (Zeigenfuss et al., this volume). On the Big Thompson River, the estimated number of beavers was 315, 102, 18 and 12 in 1939, 1964, 1980 and 1994–1998, respectively. Most of these beavers were in Moraine Park. Values reported for the Fall River in Horseshoe Park were 96, 24 and 6 in 1939, 1980 and 1994–1998, respectively.

Digital Map Generation

Low-Resolution Digital Maps

Digital maps of Moraine and Horseshoe Parks were created from interpreted aerial photos obtained for different years (Table 1). Aerial photos were scanned, geo-registered, and interpreted, rectified and digitized on a high-resolution computer screen. Photos were scanned with a 600-dpi resolution and the generated image files were geo-registered based on x-y UTM coordinate points. UTM coordinates of prominent features such as trees or road intersections were registered with a global positioning system (GPS) (Trimble Pathfinder Professional) with an error lower than 2 m. For image geo-registration, 18 and 30 GPS points were used in Moraine and Horseshoe Parks, respectively. GPS locations were uniformly distributed throughout the area of interest. A 2-degree polynomial geometric correction procedure, available in ERDAS-IMAGINE Software (1998, Version 8.3), was used to geo-register the 1996 image files based on GPS locations. Aerial photos older than 1996 were registered using the corrected 1996 images as a reference. Vegetation and hydrological features were digitized using ARC/EDIT module of ARC/INFO Software (version 7.0; ESRI 1994) program, employing the digital photos as a background image. This procedure greatly increases the possibility of identifying features, allowing both margins of river channels to be digitized.

Vegetation was classified in five classes, namely: open, meadow, riparian shrub, aspen (*Populus tremuloides*), and forest (*Pinus* spp.). Areas with a high percentage of bare soil were included in the open class; areas dominated by grasses were considered meadows. Since willow and birch, the two shrubs that grow in these riparian areas, could not be separated in the photo-interpretation, they were included in the riparian shrub class. Hydrological features were also delineated from the aerial photos. Main river, temporary and old river channels, and ponds were digitized. All channels that contained water were considered main river. Branches or meanders of the river that did not contain water were classified as temporary or old if they were wet or dry, respectively.

High-Resolution Digital Maps

During the summer of 1998, we surveyed the same areas covered in the low-resolution maps in Moraine and Horseshoe Parks. Aerial photos of these valleys taken in 1996 (Table 1) were used as a guide to organize the survey. Homogeneous vegetation patches were identified in the field by visual observation, and a GPS unit was used to delimit its boundaries. The number, as well as the size, and shape of the patches were determined according to the vegetation characteristics, in order to minimize within patch heterogeneity. Hydrological features such as main river, lakes, or ponds were mapped following the same method. We walked along the

Table 1. Aerial photography used to map willow cover and river in the two study watersheds.

Year	Site	Map type	Scale	Film type	Commissioning agency
1937	Moraine Park	River	1:22,000	Black & White	U.S. Forest Service
	Horseshoe Park lower area of the valley	Vegetation-river	1:20,000		
1946	Moraine Park	Vegetation	1:20,000	Black & White	U.S. Forest Service
	Horseshoe Park, upper area of the valley	Vegetation-river	1:20,000		
1996	Both watersheds	Vegetation-river	1:28,000	Color	Rocky Mountain National Park

boundaries of every vegetation patch or hydrological feature with a GPS unit set to digitize lines. Since the focus of the studies was on willow cover, the boundaries of the survey area were defined by the extent of willow distribution. However, some patches without willow plants occurring between the extent of the willow distribution were also delimited. GPS digital data and the associated attribute information were incorporated in ARC-INFO Software (version 7.0; ESRI 1994) to generate polygon coverages. The final error of the GPS-generated lines was lower than 2 m after correcting the data for the distortions that are purposefully introduced by the satellite system.

As in the case of the low-resolution maps, vegetation patches were primarily classified according to the general characteristics of the vegetation. A more detailed classification system was created to identify vegetation classes and subclasses. Further, in those patches where willows were present, additional attributes were registered. Four groups of species were recognized in the woody strata, namely: willow (*Salix* spp.), birch (*Betula* spp.), conifers (*Pinus* spp.) and aspen (*Populus tremuloides*) (Fig. 1). Patches without woody strata or with few sparse woody individuals were included in the meadow class. Woody vegetation classes were distinguished based on the dominant and co-dominant species. The group that presented the highest density in a patch was considered dominant, without regard to the overall woody strata density. Other groups occurring in a patch were co-dominant. Groups comprised of isolated individuals in an overall high-density patch were not considered in the classification. Since visual observation was used to delimit and classify vegetation patches, there was no quantitative value for the minimum number of plants determining if a group should be classified as co-dominant, or not included. Nevertheless, ambiguous cases were rare, because no more than two groups occurred in most patches. Since the survey was targeted on willow areas, some vegetation classes such as meadow were only partially surveyed (particularly one large meadow in Horseshoe Park, and several meadow areas in Moraine Park). Forest and aspen vegetation classes were separated from the riparian vegetation. Consequently, they were seldom included in the survey. Only willow and birch were completely surveyed.

Additional attributes were used to describe the heterogeneity in willow cover in more detail. Four categories were defined to characterize the morphological characteristics of: (a) dominant, (b) co-dominant willow morphotypes, (c) density, and (d) percentage plants dead (Table 2). As previously described, this classification was

based on visual estimations. A zero value was assigned in all of the four categories in the case of patches without willow plants. Density was estimated considering both live and dead willow plants. The morphotype that presented the highest density in a patch was considered dominant and the second most common morphotype was considered co-dominant. Only one morphotype was included in the co-dominant categories to make the classification simpler.

Height difference was the primary attribute used to discriminate willow morphotypes, but more detailed observations were made to differentiate between saplings and young short willow, and between young and old short willow. We considered saplings to be individuals that were recently established (4–5 years) from seeds or vegetative reproduction, but not from resprouting of old individuals. Areas with high density of willow saplings, and without woody strata, were classified in the meadow-willow vegetation subclass (Fig. 1). We identified willow saplings using several morphological characteristics such as height shorter than 50 cm, small basal diameter of the largest stem (around 5 mm), brownish stem without sign of lignification, and small crown size relative to the size of the plant. These latter characteristics indicated that plants were not sprouts from old individuals. Additionally, some of the largest stems were dated based on the ramification pattern, and were between 4 and 5 years old. The young willow category included plants that were similar in height to short willow morphotypes (approximately 1.5 m in the case of tallest plants). Mature plants were composed of several large stems and consequently had crowns several times larger than plants considered as saplings. The largest stem diameter in short young willows was on the order of 1.5 to 2.0 cm. These plants looked younger than other short willows, as indicated by the brownish color of the stem that contrasted with a white color typical of old stems of old willow plants. Additionally, no dead stems, in particular old dead stems, were found inside or between the canopies of young plants, as were commonly found in older short willow stands. This distinction was made to infer dynamics occurring within the short morphotypes.

Patches comprised of saplings or young short willows were interpreted differently if other morphotypes were or were not present in the patch. If patches with a high density of saplings or young short willows occurred together with other willow morphotypes, they were interpreted as areas originally covered by willow with high recruitment. Areas dominated by saplings or young short willow, in which no other dead or live willow morphotypes were present, were considered to be areas

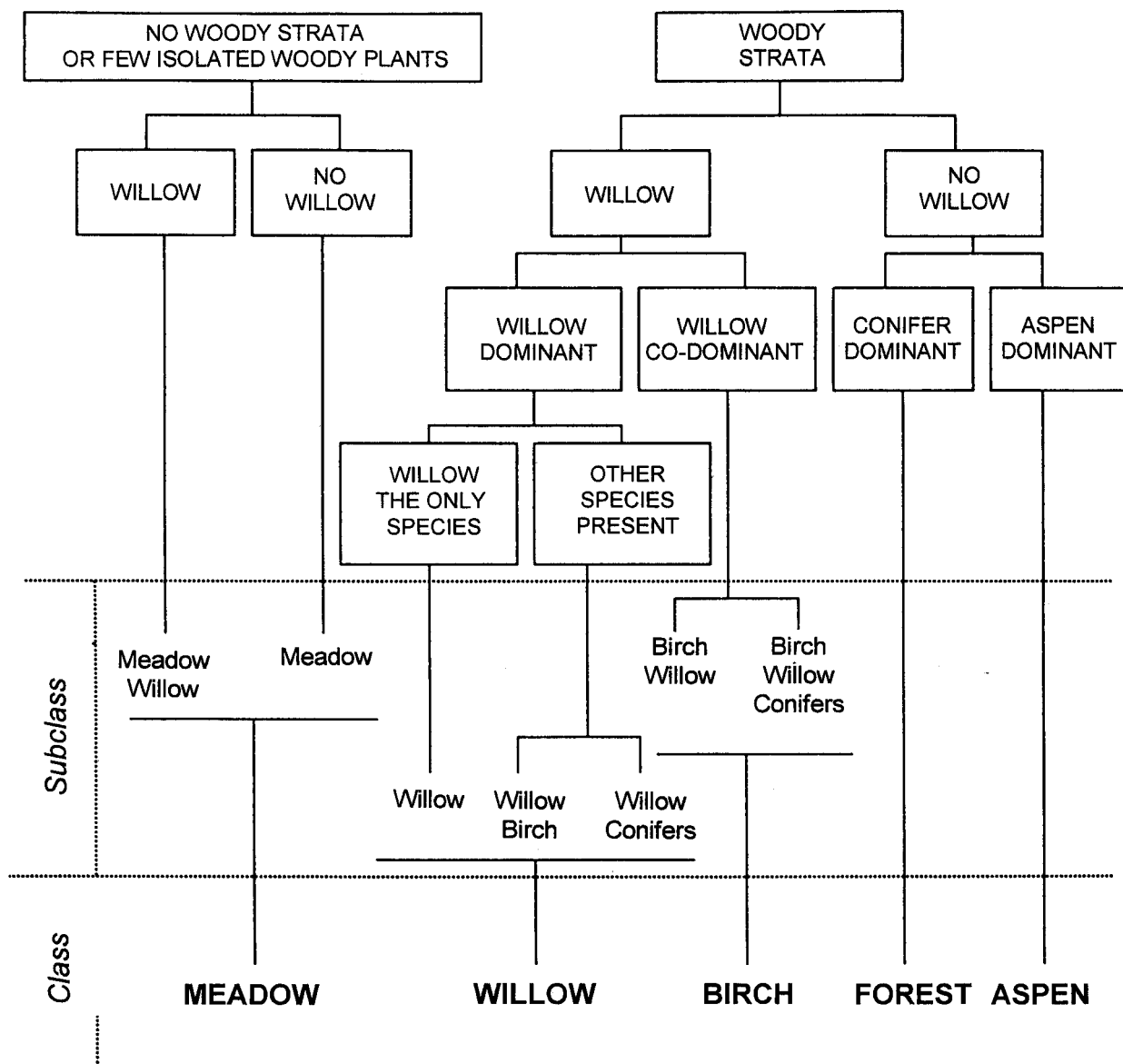


Fig. 1. Schematic of vegetation class and subclass classification.

Table 2. Description of categories used to classify patches that contain willow.

Category	Values	Description
Dominant willow	0. No willow	
Codominant willow	1. Sapling	Less than 0.5 m tall
	2. Short young	0.5 to 1.5 m tall, young stems
	3. Short old	0.5 to 1.5 m tall, old stems
	4. Intermediate	1.5 to 2.0 m tall
	5. Tall	Greater than 2.0 m tall
Willow density	0. No willow	
	1. Few willows	Sparse willows
	2. Low density	Distance between plants around 5 m
	3. Moderate density	Distance between plants around 3 m
	4. High density	Distance between plants less than 2 m
Dead willow	0. No willow	
	1. Less than 10%	
	2. 10 to 30%	
	3. 30 to 50%	
	4. 50 to 80%	
	5. Greater than 80%	

recently colonized by willows. These patches were classified as “new colonization” if only saplings were present and were interpreted to be areas that had been colonized less than or equal to 4 or 5 years ago. Similarly, patches that contained young short willows and saplings, but not other morphotypes, were interpreted as an older colonization (older than 5 years), and designated in the maps as “colonized several years ago”.

Data Analysis

Changes in willow vegetation were interpreted relative to hydrological changes and historic events. GIS data from the low-resolution maps were used to examine the transitions in riparian shrub cover. Willow was the most common shrub in these watersheds, so we assumed that the riparian shrub class was mostly composed of willows. GIS data were derived from 1998 field surveys by aggregation of detailed vegetation attributes. Willow cover was estimated based on three criteria resulting from a combination of different attributes used to classify

willow patches (Table 3). The first criterion considered willow cover to be patches in which willow plants were present. Since this was the least strict criterion, it gave the highest values of total willow cover and was used to calculate percent cover of the different willow types. The second criterion classified willow cover as areas where willow was the dominant vegetation type. A third and stricter criterion classified willow cover as woody areas dominated by willow with a high density of living individuals.

Cover areas of riparian shrub classes from maps created by the interpretation of old and new aerial photos were compared. The minimum resolution of the photo-interpretation was inferred by overlaying low and high-resolution maps. In this way, the minimum map resolution in the photo-interpretation was defined based on the characteristic of the vegetation in the high-resolution maps, namely dominant group, density, and percentage of dead plants. This procedure allowed us to determine characteristics of the low-resolution polygons based on the attributes recorded in the high-resolution maps.

Table 3. Total area (ha) covered by willows in the surveyed watersheds according to three different criteria. Values in parentheses indicate percent covered using criteria 1 (willows present).

Criteria	Classification			Area covered (ha)	
	Vegetation class	Vegetation subclasses	Willow category	Moraine Park	Horseshoe Park
1 Willows present	Not specified	Not specified	Dominant willow >0	104.5 (100)	88.3 (100)
2 Dominant vegetation	Willow	Not specified	Not specified	71.6 (68)	72.4 (82)
3 High density Low dead percentage	Willow	Not specified	Willow density = 3 or 4 Dead willows = 1 or 2	50.0 (48)	65.3 (74)

Results

Low-Resolution Digital Maps

Important hydrological changes, including reductions in the complexity of the river pattern and in total surface water, were found in both watersheds. Changes were more pervasive in Moraine Park, where the length and water surface area of the main channel were reduced by 56% and 69%, respectively (Table 4). Most changes in the river course occurred in the south main branch of the river (Fig. 2). By 1996, the river channel had almost no branching and most of the temporary river courses had disappeared. The complex pattern of the river observed in 1937 was most likely the result of beaver activities, but it was difficult to identify beaver ponds. All ponds that were identified in the 1937 and 1996 maps (Fig. 2) were not a result of beaver activities. Beaver created several dams that produced small impoundment areas, but the main impact of beaver appeared to be an increase in river ramification and meanders. Most of the 1937 river channels that had disappeared by 1996 could not be identified in the photos. Flooded areas on wet meadows were evident in the central part of the Moraine Park valley in both years, but were more extensive in 1996 (Table 4). In Horseshoe Park, the length and surface water of the main channel of the river in 1996 were reduced to 44% and 47%, respectively, of the values observed in 1937–1946 (Table 4). The main reduction in river complexity occurred in the upper reaches of the valley (Fig. 3). Several ponds created by beaver could be clearly identified on the old photos. These ponds disappeared by 1996. Important hydrological changes had also

occurred in this valley, produced by a 1982 flood event. Changes in the lower part of the valley did not appear to be as important as in the upper areas, but the river pattern became less meandering by 1996.

Changes in spatial patterns and a decline in the total area covered by riparian shrubs were determined in both watersheds. The reduction was 21 ha (21%) in Moraine Park during the span of 50 years, and 17 ha (19%) in Horseshoe Park during the time spans of 50 and 59 years (1937 and 1946 aerial photos; Table 1). In Moraine Park, riparian shrubs covered 101 ha in 1937 and 80 ha in 1996. Changes in shrub cover occurred mostly in the wider part of the valley (Fig. 4). The two narrow valleys in the upper areas of Moraine Park (west) did not show any important change. Compared to the spatial pattern of willow cover delimited in the 1946 photos, willow in the northwest part of Moraine Park slightly increased over meadows, and the forest area also became larger. It is important to consider that in these two narrow valleys there is an ecotonal zone in which riparian areas dominated by willow are replaced by birch and forest. These transitions were difficult to delimit from the photos. Wider areas of the watershed in Moraine Park showed major changes in willow cover. Decreases in willow cover were spatially associated with reductions in river meanders and small impoundments. Some meadow areas identified in the 1996 map were previously covered by willow.

In Horseshoe Park, willow cover was reduced from 90 ha in 1937/1946 to 73 ha in 1996. The 1982 flood caused a remarkable change in vegetation cover in the middle of the watershed (Fig. 3). In the upper area of the watershed, where the flood had less effect, willow vegetation cover did not change noticeably, but there

Table 4. Length (km) and surface area (ha) of hydrological features in Moraine Park in 1937 and 1996 and Horseshoe Park in the combined years of 1937/1946 and 1996.

	Moraine Park				Horseshoe Park			
	Length		Surface area		Length		Surface area	
	1937	1996	1937	1996	1937/1946	1996	1937/1946	1996
Main river	30.2	13.3	23.8	7.5	16.8	9.4	9.7	5.1
Current meanders	12.1	6.9	10.1	2.6	0.5	1.8	0.2	1.0
Old meanders	3.0	0.3	2.5	0.1	2.2	2.3	0.8	1.6
Ponds	-	-	1.4	1.0	-	-	10.9	47.6
Flooded areas	-	-	4.6	21.4	-	-	-	-

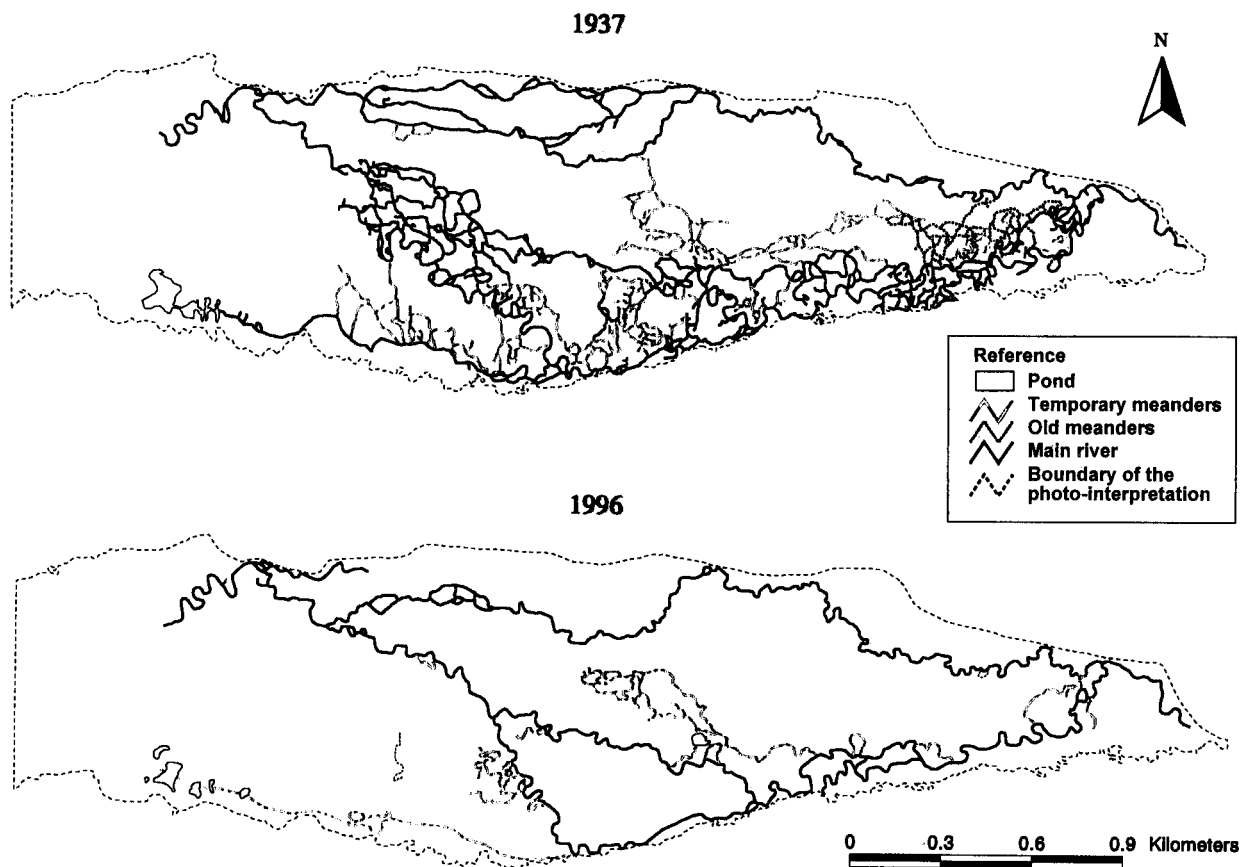


Fig. 2. Hydrological maps of Moraine Park in 1937 (upper map) and 1996 (lower map) determined using low resolution digital maps based on aerial photo interpretation.

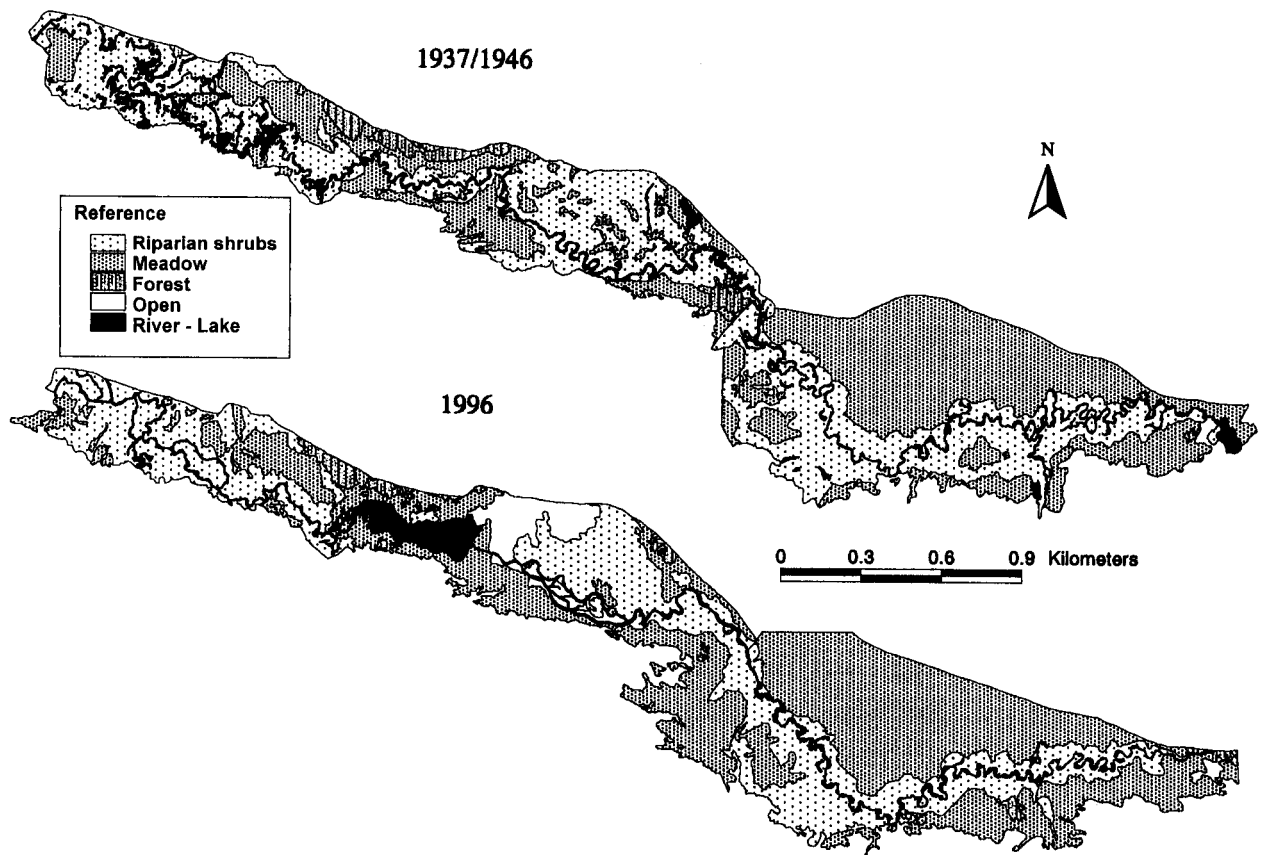


Fig. 3. Spatial distribution of vegetation classes and hydrology in Horseshoe Park in 1946, in the upper part of the valley and in 1937 in the lower part of the valley (upper map), and the same area in 1996 (lower map). Maps were created using low-resolution digital maps based on aerial photo interpretation.

was an important reduction in the total impoundment areas. Unlike Moraine Park, the reduction in surface water was not associated with a willow cover decline. Changes in willow cover in the lower part of the valley were not as spatially localized as in Moraine Park. Some willow stands were replaced by meadows, and a minor proportion was replaced by forest.

High-Resolution Digital Maps

Vegetation maps of Moraine and Horseshoe Parks produced by the ground-based GPS survey (Fig. 5) were similar to the 1996 low-resolution air photo maps (Figs. 3 and 4). Although, some meadow and forest patches were not delineated in the GPS based maps, more details in the riparian shrub cover were included. The shrub

vegetation class was separated into areas dominated by birch and willow. The birch cover class was greater in Moraine Park than in Horseshoe Park (18 ha and 0.7 ha, respectively). Birch cover was mostly restricted to the south part of Moraine Park in the area where major changes in the river channel were documented. The three different methods used to classify willow cover produced markedly different estimates of willow in Moraine Park but not in Horseshoe Park (Table 3). This indicated that the spatial pattern of willow cover was more complex in Moraine Park than in Horseshoe Park.

Willow cover was very heterogeneous. Observed combinations of area types and willow categories ranged from areas in which willow were decreasing and had a high percentage of dead individuals, to meadows or open areas, that had been colonized by willow during the last few years (Table 5). Dead willow areas were more

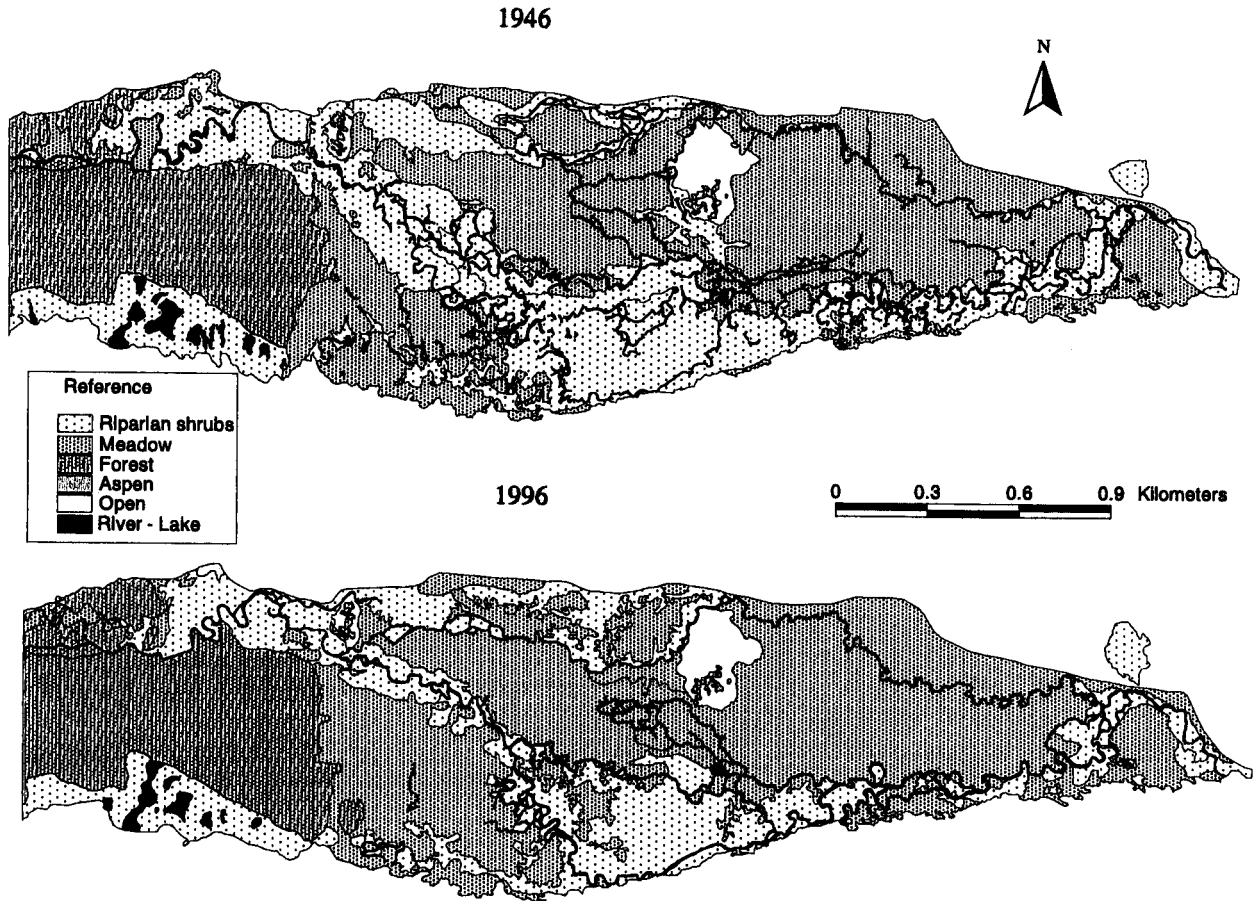


Fig. 4. Spatial distribution of vegetation classes and hydrology in Moraine Park in 1946 (upper map) and 1996 (lower map), determined using low resolution digital maps based on aerial photo interpretation.

extensive in Moraine Park than in Horseshoe Park (Table 5 and Fig. 6). In Moraine Park, these areas were dominated by tall willow as evidenced by the high number of dead willow with large crowns, and several tall stems that remained on the plant. Some of the live willows were also tall, but with several dead stems indicating stressful conditions for willow growth. Many old river channels and old signs of beaver activity were found in the two largest dead willow polygons. On the contrary, only a few patches dominated by dead willow were found in Horseshoe Park (Fig. 6). New and old willow colonization was found in both parks. These areas were more extensive in Horseshoe Park (34% and 12%, respectively), but some of them had a low density (Table 5). In Moraine Park, the major areas colonized by willow were on a meadow that received water diverted

from the northeast branch of the river by beaver disturbances. These areas corresponded in part to some of the flooded areas identified in the low-resolution maps (Fig. 2). Flooding was produced by beaver activity. Beaver dams apparently reduced water flux in the main channel, resulting in a ramification of the river into several small channels. Although there was evidence of new beaver cuts on willows, beaver did not seem to maintain the dams. Under high water flow resulting from snowmelt (June and July), water moved out of the channel and into the meadow. This water was ultimately routed to the southern main branch of the river. Water flow through the meadow was gone by August in the summer of 1998. Several willow saplings were established in this area under conditions of soil water saturation. In Horseshoe Park, new willow colonization

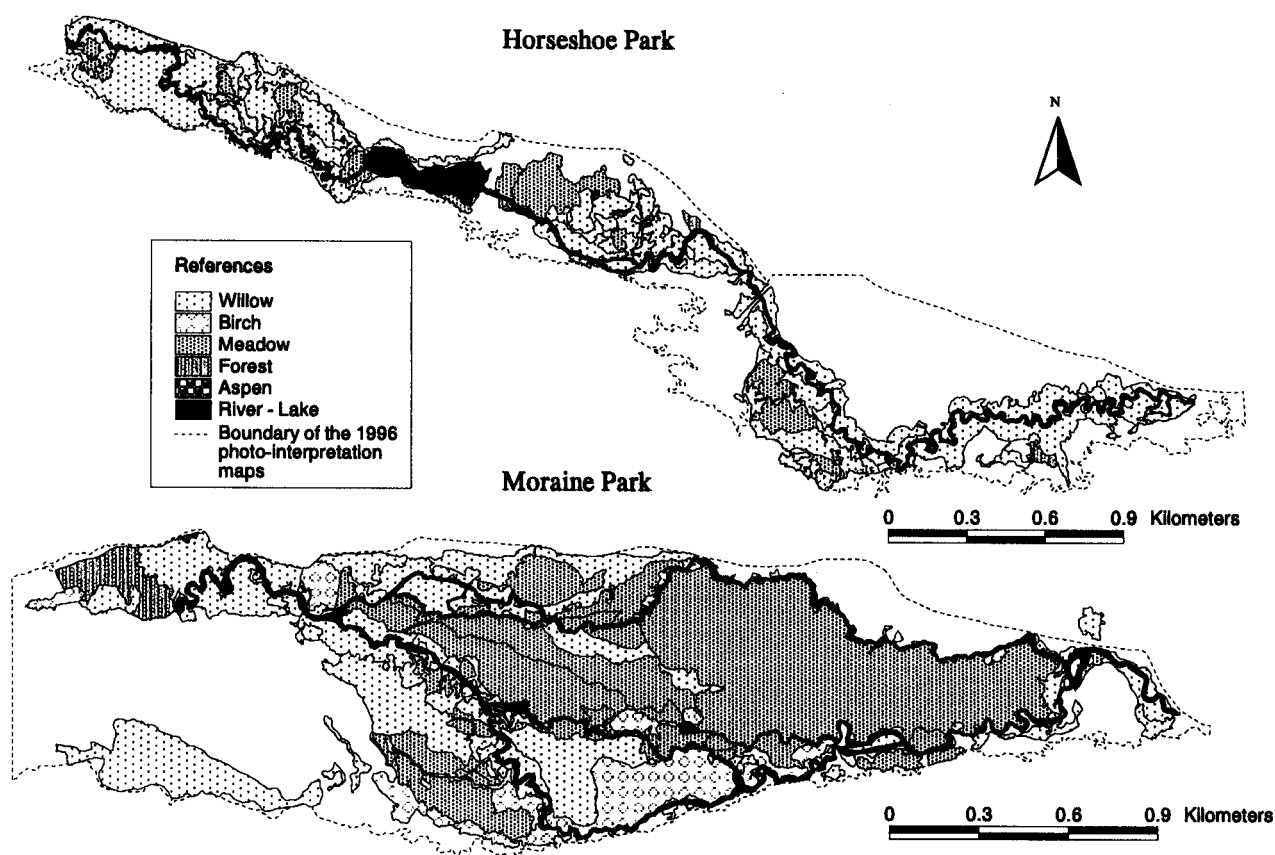


Fig. 5. Spatial distribution of vegetation classes in Horseshoe Park (upper map) and Moraine Park (lower map), determined using high resolution digital maps based on field mapping.

was found on the alluvial fan created by the 1982 flood (Fig. 6). Willows were also colonizing several meadows in the upper areas of the valley. Evidence of old colonization was also found in meadows of both the upper and lower parts of Horseshoe Park. Several small patches with high willow recruitment were found in areas temporarily flooded by the river in both watersheds.

Differences in willow morphotypes were the other source of heterogeneity in willow cover. Short old categories were abundant in Horseshoe Park (Table 5), but most of the short willows in Moraine Park occurred at low densities in the south-central part of the watershed. These areas were classified as areas covered by low willow density (Table 5). If low-density dead willow is included, the total cover of the short old morphotype increases considerably in Moraine Park but not in Horseshoe Park (Table 5). Short morphotypes were on

the areas where major reductions in river channels were documented, indicating that these morphotypes occurred in areas of unfavorable growing conditions.

Tall willow was more abundant in the upper areas of the valley in both watersheds (Fig. 7). Changes in river course were probably less important in these upper areas because the river is constrained to a narrow valley. The tall willow polygon in the southwest part of the valley in Moraine Park has many ponds (not shown in the GPS maps) and saturated soils, which create favorable conditions for willow growth. Even though major changes in surface water were documented in the upper part of the valley in Horseshoe Park, no shift to lower willow cover or larger cover of short old morphotypes had occurred. In the lower valley of Horseshoe Park, tall morphotypes tended to be more abundant in areas farther from the river course.

Table 5. Total area covered by willow (ha) according to criteria 1 in Table 3, divided into different area types and willow categories. Percentage of total willow cover in parentheses.

	Area type	Willow categories				Area covered (ha)	
		Dominant	Codominant	Dead	Density	Moraine Park	Horseshoe Park
Colonization							
New	Saplings	Young	None	Low	Any	8.4 (8)	3.0 (3)
Old	Short young	Short Young	Young or none	Low	Low	0.02 (0)	12.2 (14)
					High	4.2 (4)	14.8 (17)
Areas originally covered by willow							
	Short old	Short old	Any	Low	High	10.1 (10)	18.7 (21)
	Intermediate	Intermediate	Any	Low	High	7.6 (7)	4.1 (5)
	Tall	Tall	Any	Low	High	28.3 (27)	30.4 (34)
	Dead willow	Any	Any	High	High	17.6 (17)	2.1 (2)
	Low density	Any	Any	Any	Low	28.3 (27)	3.2 (3)
Total						104.6 (100)	88.3 (100)

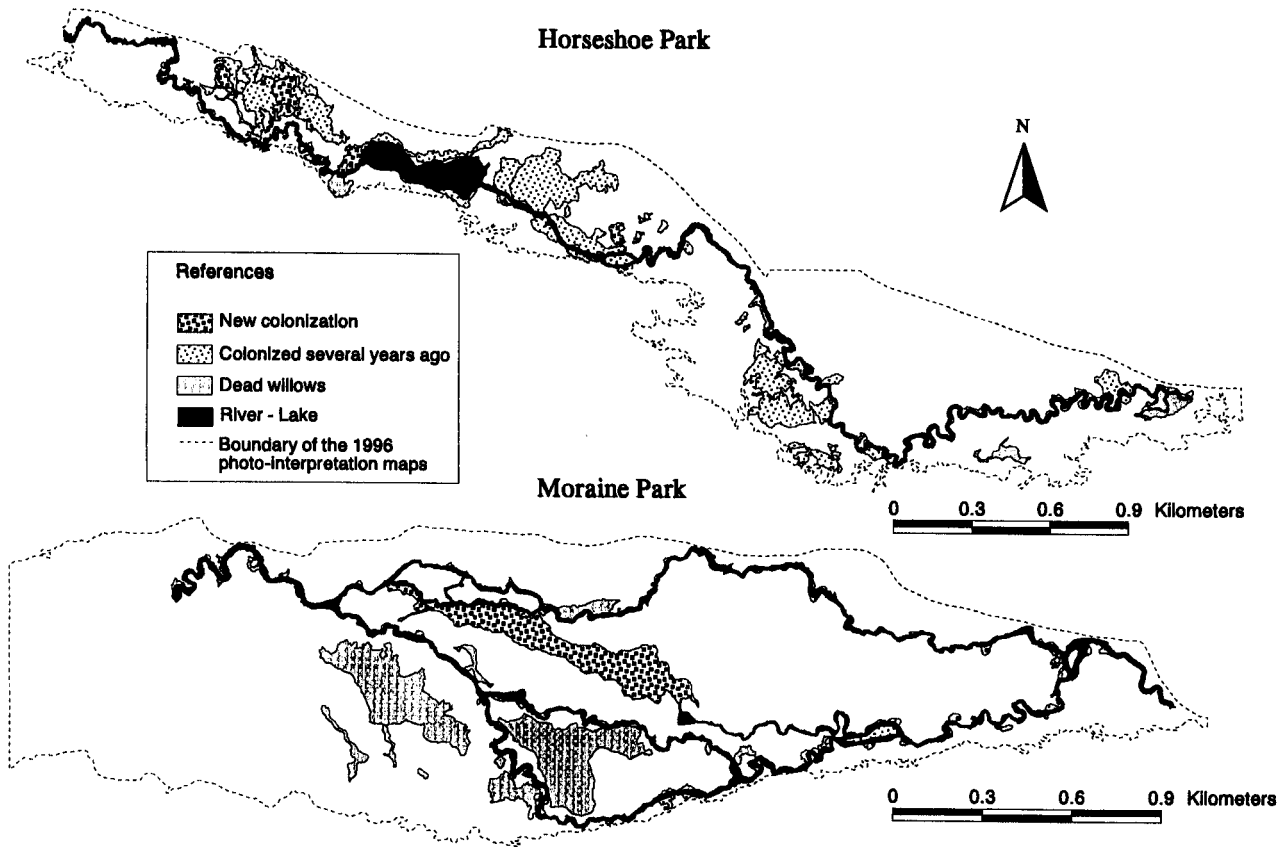


Fig. 6. Spatial distribution of areas dominated by dead willows and areas colonized by willows in Horseshoe Park (upper map) and Moraine Park (lower map), determined using high resolution maps based on field sampling.

Intermediate morphotypes were found in the wider areas of both valleys more spatially associated with short old willow morphotypes.

A more complicated pattern of river channels could be inferred from the extensive evidence of abandoned branches of the river and old meanders in Moraine Park. Old meanders were also found in Horseshoe Park, but they seemed to be less frequent than in Moraine Park. A great deal of evidence of old beaver activities was found in Moraine Park, but little was found in Horseshoe Park. Few signs of new beaver activities were observed in either watershed. Only one small beaver pond was found in the tall willow area of Horseshoe Park.

Comparison Between Low and High-Resolution Maps

In both valleys, willow cover based on criterion 2 (Table 3) was similar to the riparian shrub cover of low-resolution maps. In the case of Horseshoe Park, riparian shrub cover corresponded almost exactly to the value of willow cover estimated by using criterion 2 (723,676 m² and 727,389 m², respectively). In Moraine Park, riparian shrub cover overestimated willow cover obtained with criterion 2 by 83 ha (716,012 m² and 799,471 m², respectively). The riparian shrub class included areas dominated by birch, but excluded most of the dead willow

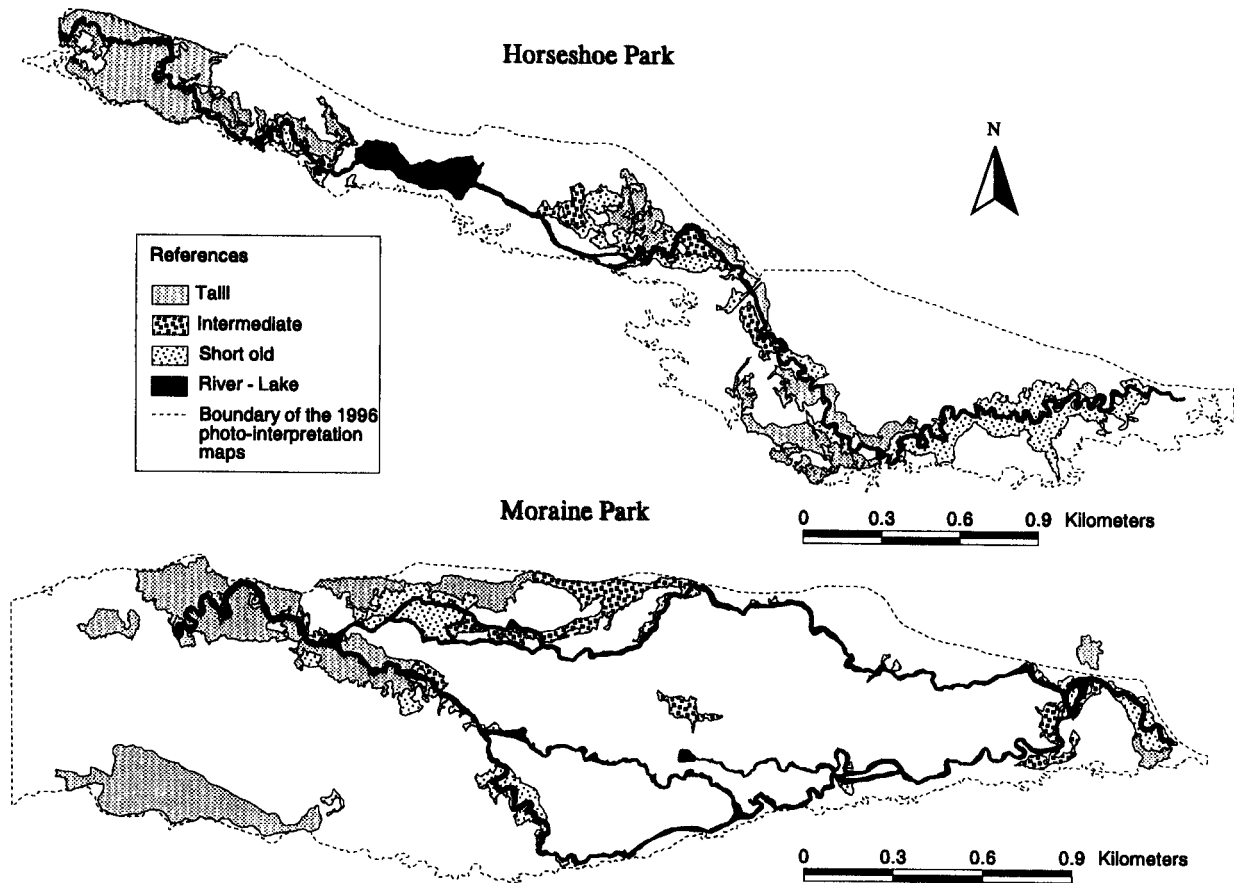


Fig. 7. Spatial distribution of willow morphotypes in Horseshoe Park (upper map) and Moraine Park (lower map), determined using high resolution maps based on field sampling.

areas. Since birch and dead willow covered a small portion of Horseshoe Park, cover values obtained from the different resolution maps were nearly the same. On the contrary, in Moraine Park, riparian cover was larger in the low-resolution map because dead willow areas could not be excluded, and cover of some of the shrub patches was overestimated.

Discussion

Geomorphological characteristics of drainage segments (reaches) have important effects on the development of riparian vegetation (Gregory et al. 1991). The upper areas of both study watersheds occurred in narrow valleys and had constrained reaches. Consequently, the position of the stream channel was

relatively fixed. Riparian vegetation in the upper areas of both watersheds was dominated by tall willow and no important changes in riparian cover occurred in these areas. Lower areas of both study watersheds had unconstrained reaches, characterized by a lack of significant lateral constraint and low streamflow gradient. This allowed the stream to form braided channels. Importantly, short willow morphotypes were mostly restricted to these lower, unstable reaches, where there were major changes in hydrology between 1946 and 1996.

Decreases in willow cover as estimated from the change analysis only took into account areas where willows disappeared. Other changes in willow community characteristics, such as the proportion covered by different morphotypes, were not included. On the 1937/1946 aerial photos it was difficult to identify

whether areas covered by riparian shrubs corresponded to tall willow, or a combination of different willow morphotypes and birches. In contrast, the GPS survey provided accurate estimates of the proportion of the areas covered by different morphotypes and birches, but only for 1996. The combination of information from the historical and recent cover maps allowed us to make two inferences about trends in willow cover over the study period. The first requires an assumption that in the old photos all of the areas classified as riparian shrubs were dominated by tall willows. From this we inferred that tall willow declines equaled 54% and 65% for Moraine and Horseshoe Park, respectively. If, in addition to the previous assumption, areas currently classified as birch are also considered to have been formerly dominated by tall willows, then the declines in tall willow become 72% and 66% on Moraine and Horseshoe Park, respectively. Changes in willow cover, such as reductions in willow density or shifts from tall to short morphotypes, could not be determined with this data. However, it is safe to say that this analysis of willow decline, based only on areas where willow disappeared, underestimated the total changes that actually occurred.

A comparison of estimates of willow decline using the two different methods (low and high-resolution) provides additional insight about the effects of disturbance. From the low-resolution maps, declines were determined based on the difference between old and recent air photos, assuming that willow were the dominant shrub species. From the GPS survey, declines were inferred based on the amount of area dominated by old dead willow plants. By comparing the two results, we found that the declines based on aerial extent of dead willow were 20% and 80% less than the estimates based on disappearance in Moraine and Horseshoe Park, respectively. This indicated that most dead willow plants remained in Moraine Park, but dead willows were removed in Horseshoe Park, probably by the 1982 flood event.

Even though changes to drier climatic conditions (Singer et al. 1998a), could have affected willow growth and productivity, lower precipitation did not seem to be the primary causative factor producing the observed willow decline. Both valleys experienced a drier climatic trend, but showed different willow cover dynamics. Water used for willow growth came mainly from groundwater rather than current precipitation (Alstad et al. 1999), and the level of the water table was mainly regulated by the hydrological characteristics of the river (Patten 1998). Willow growth would not be affected by decreased precipitation, as long as the water table level remained high. In this way, many willows could be buffered from

a slightly lower precipitation. However, since the depth of the water table during the willow growing season is mostly determined by the winter snowpack accumulations and the spring-summer melting rate (Patten 1998), it is also possible that water tables were reduced, or of shorter duration, under climate change.

As expected, changes in hydrology were a critical factor in determining willow colonization and population persistence in both parks; however, hydrological changes were different between parks. In Moraine Park, willow disappeared from areas where major reductions in river complexity were documented. In 1996, the main channel of the river was simpler, and well delimited compared to 1937/1946. Although this could have been the result of reduced water flow, the previous high river complexity and impoundment areas were clearly the result of beaver activities. Well-defined beaver dams surrounded by riparian shrubs were found in the upper Horseshoe Park valley in 1937/1946. Almost all of these ponds disappeared by 1996, but no noticeable changes in riparian shrub vegetation were documented as was observed in Moraine Park.

These contrasting responses of the riparian shrub community to decline in beaver could have resulted from differences in interactions between basin geomorphology and beaver activities. Johnston and Naiman (1987) distinguished the characteristics of beaver dams in upland V-shaped valleys from wetlands with extensive floodplains. Beaver dams in upland streams produced small ponds with well-defined contours. In these ponds, there was little change in surface water level when stream water level fluctuated. In wetland floodplains, small beaver dams often inundated a large surface with shallower water depth and the pond boundary was diffuse. Beaver alterations seemed to have less impact on ecosystem level processes in wetlands than on uplands because soils in wetlands were under saturated conditions (Johnston and Naiman 1987). Well-defined beaver dams were found in the upper areas of Horseshoe Park, in the V-shaped part of the valley. There, the water table was probably not reduced by the decrease in beaver and their ponds, because the water table was controlled by geomorphology more than by beaver ponding. If this was the case, then hydrological conditions for shrub growth were little affected by the beaver decline.

Floodplains of both watersheds represented conditions that were intermediate between the two contrasting situations just described. On floodplains, geomorphic characteristics were similar to a valley with a low elevation gradient, but soil water saturation could occur only during a short period of time, in a restricted

area close to the river. Water tables, in areas close to the river, fluctuated between 20 cm and 100 cm during the annual peak in stream flow (June) (Zeigenfuss et al., this volume). In this situation, beaver dams noticeably changed the hydrological conditions for vegetation growing around edges of ponds. Although ponds did not have a defined boundary as in the case of wetlands, they were not large. The gradient of the floodplain in Moraine Park was large enough to limit the size of the pond because further increases in pond surface area were limited by the formation of a new drainage channel. In this valley, well-defined beaver ponds were difficult to identify in 1946, but there were several small impoundment areas and many branches of the river.

This hydrological process ultimately increased the branching pattern of the river, and probably resulted in a larger area of water subsidization than would occur with a few large beaver ponds. Thus, decreases in beaver abundance caused a simplification of the river course and a reduction in the area of land surface influenced by the river and associated water tables. In areas where water tables were diminished, drier conditions prevailed, and riparian shrub communities were replaced by meadows.

Willow decreases in Horseshoe Park seemed to be, in large part, caused by the flood disturbance following the collapse of an earthen dam in 1982. Most of the reduction in riparian shrub cover occurred on downstream areas that were directly affected by the flood. In 1996, areas with bare soils created by the flooding were being colonized by willow. Periodic large flood disturbances that destroy vegetation and generate open patches for plant establishment have been considered to be important in models of riparian landscape structure (Miller et al. 1995). Some riparian species depend on these recurrent disturbance events for establishment. Thus, alterations of the flood regime have negatively affected many riparian ecosystems (Bradley and Smith 1986).

The flood event that occurred in Horseshoe Park produced a larger disturbance than normally expected in a recurrent flood regime in mountain valleys (Patten 1998). The hydrological characteristics of the river were not only altered downstream but also upstream, through a large mass of rocks and boulders that slid into the valley (Jarret and Costa 1993). Restriction of river flow in the area of the alluvial fan could have increased water tables in the upper areas of the valley. This is the area where major reductions in beaver ponds were found.

In addition, water table levels in the meadows that were colonized by willow in the upper areas of the valley (Figs. 3 and 6) could have increased since the flooding,

producing favorable conditions for willow establishment. Willow seedlings rapidly colonized the sediments deposited in the alluvial fan in the summer of 1983 (Keigley 1993). Even though some patches contained a high density of seedlings, few of them survived to the following years (Keigley 1993). Most of the willow observed on the alluvial fan in 1998 came from the original establishment of 1983 (Keigley 1993). This area was classified in the GPS survey as being colonized several years ago because it was dominated by young short willows (Fig. 6). These willows were no older than 15 years.

Willow produces wind-dispersed seeds that have a limited viability and no willow seed bank ever develops (Raven 1992). In RMNP, tall willow normally produce a large number of seeds and seed availability does not limit willow establishment (Cottrell 1995). Willow saplings (younger than 4–5 years) were observed in meadows with high soil water content indicating that recruitment is not restricted to bare soil as occurs with other riparian species (Bradley and Smith 1986). However, wet sandbars are suitable sites for willow establishment, as indicated by high recruitment observed in areas affected by flooding.

The study areas have been intensively affected by human activities since the late 1800s. Important changes could have occurred in riparian communities before the area became part of the national park. Nevertheless, during the period covered by this study, the impacts of human activities on riparian communities decreased because the area became protected under national park policy. However, in the last 50 years, both watersheds have shown signs of deterioration in the riparian plant communities. These changes do not seem to have been caused by direct impacts on the ecosystem. However, humans may have generated conditions that led to increased elk population size, which could have affected the riparian ecosystem.

The large proportion of willows with short morphotypes in 1996 could be a result of increased elk browsing. Elk browse on willow mainly during the winter, on the new shoots developed during the previous growing season. An increase in elk browsing on willow leaders could produce suppressed willow morphotypes. In a similar way, high elk browsing pressure inhibits height elongation on young aspen stems, and suppressed plants are preferentially browsed by elk (Romme et al. 1995). Tall plants are protected from browsing because new meristems are beyond the reach of elk. Disturbances, such as flooding or beaver activities, facilitate elk access to willow shoots. Interestingly, in Horseshoe Park, short

and intermediate willow morphotypes were primarily located in the downstream flooded area. Disturbances might open up the willow canopy, stimulating stem turnover. Elk could then access new stems causing an increase in the density of stems with a suppressed morphology. This process would ultimately lead to a short willow community. Additionally, young willows growing under heavy browsing levels will be kept in a short morphotype. It is expected that under heavy browsing, areas newly colonized by willow will be primarily comprised of short morphotypes, thus increasing the total area of short willow.

Elk browsing pressure on willow increased following reintroduction and cessation of artificial controls, but it is not clear how this could have affected the extent of willow cover. We hypothesize that increased elk browsing did not directly cause a long-term decrease in riparian shrub cover but may have indirectly contributed to the decline. All of the areas where willow disappeared suffered important hydrological changes. A willow cover decline was also found in Yellowstone National Park (Engstrom et al. 1991), where a similar interaction between elk and drier conditions had occurred (Singer et al. 1998a). During the 1988 drought in Yellowstone, willow in two stands located on dry marginal sites died. Willows in one stand were heavily browsed but willows in the other were not (Singer et al. 1994). Under a long-term trend of reduced water availability, other vegetation types will replace riparian shrubs, since they are not adapted to withstand water stress (Patten 1998). Under this scenario, differences in the level of elk browsing on willow would make little difference in the long-term vegetation trend. Thus, elk could have reduced willow canopy cover within a willow patch by suppressing plant growth, but the total area covered by willow in the valley would be primarily controlled by the amount of wet habitats suitable for riparian vegetation growth. However, elk could indirectly affect beaver by reducing the extent of tall willow morphotypes. Beaver decreases induced the reduction of river length and water subsidized surface area, causing drier conditions for willow growth. It is not clear why beavers have almost disappeared from these RMNP watersheds, but it is possible that the elk increase contributed to the beaver decline.

Direct species interactions (physical interaction) have been most commonly studied, but recently, indirect effects have been shown to be important in many studies (Wootton 1994; Schmitz et al. 1997; Olff and Ritchie 1998). Beaver have a direct effect on riparian shrubs by cutting stems that are used for food or building dams

and lodges (Nolet et al. 1994). Additionally, beaver impoundments create favorable physical conditions for riparian vegetation growth (Naiman 1988; Johnston and Naiman 1990b,c). Shrub reinvasion has been observed in abandoned beaver ponds (Remillard et al. 1987). Fragmentation of willow plants and the movement of the cut stems by beaver could be an important factor in the asexual propagation of the species (Cottrell 1995). At the same time, a direct interaction occurred between elk and willow. Changes in willow communities induced by elk, such as increases in cover of suppressed morphotypes, will have indirect negative effects on beaver. One of the major challenges in ecology is the identification of the strength of species interactions (Wootton 1994; Bertness and Leonard 1997). The signs and intensities of the interactions are dynamic. They depend on the size of the beaver and elk population, as well as the characteristics of the riparian vegetation and environmental conditions. Plant biomass production responses to different levels of browsing (Bergström and Danell 1987), beaver cutting (Kindschy 1989), and biogeochemical changes induced by elk or beaver also need to be considered (Naiman and Melillo 1984; Pastor and Naiman 1992; Hobbs 1996). Species interactions, particularly between beaver and willow, seem to be an important source of stability in these riparian ecosystems, which are subject to continuous disturbance events. These ecosystems are largely dependent on beaver, which act as a keystone species (Bond 1994; Heywood 1995) generating favorable conditions for willow growth. Thus, persistence of these riparian communities will depend on the reestablishment of the biotic and abiotic conditions that support beaver populations.

Conclusions

Trends in willow cover were similar in both parks, but the characteristics of the decline and conditions of the current vegetation were different. In Moraine Park, riparian shrub declines were spatially associated with major reductions in river complexity. In Horseshoe Park, declines were mainly spatially associated with areas that were directly affected by the 1982 flood disturbance. Willow vegetation in Moraine Park was more heterogeneous than in Horseshoe Park. This heterogeneity was caused by a high proportion of short willow morphotypes that grew in low density in areas dominated by birch and dead willow cover. Willow colonization was found in both parks on wet meadows and also in areas affected by flooding in Horseshoe Park.

The potential causes of willow decline are many, but it is clear that beaver played a role in increasing riparian habitat cover by increasing stream channel complexity, creating impoundments of water, and thus increasing the area of land surface where there is an elevated water table. The decline in beaver between 1939 and 1969 is not well quantified, and the available data indicate that there were still many beaver present in 1969. It would be useful, therefore, to conduct an additional willow survey using 1969 aerial photography, to try and determine how much of the willow decline occurred before or after 1969.

Humans may have played a role in decreasing riparian habitat, through their activities between 1875–1961, including substantial alterations of the hydrology through ditching in Moraine Park. Despite these alterations, however, beavers were still present in abundance in 1939 and to a lesser extent in 1969. Horseshoe Park was not affected this way, yet there was still a decline in willow cover, and a shift to shorter morphotypes. There is a need to try to reconstruct human activities and their effects more precisely.

Elk wintering in RMNP increased in number from 0 in 1914, to at least 800 in 1943, were kept at 600 or below 1944–1968, and then increased to over 1,000 in the late 1980s. Yet, studies indicate that willows are well adapted to tolerate herbivory. Willows were still abundant in 1939–1946, when there were also abundant elk. There may also have been abundant elk prior to their extirpation through market hunting. Climate data suggest a slight warming and drying, but the impacts of such a climate shift on hydrology and riparian habitats have not been determined. In our opinion, decreases in the area of riparian, water-subsidized habitat resulting from beaver decline have probably been much more significant than either changes arising from elk herbivory alone, or from lower precipitation. The cause(s) of the beaver decline are still unknown. There is a need to evaluate alternative explanations which might include: disease outbreak; beaver overabundance and resultant crash due to loss of forage; competition with elk; and loss of habitat and forage due to human land use and hydrologic alterations.

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